

## TRADE-OFF BETWEEN MALE REPRODUCTION (AMPLEXUS) AND GROWTH IN THE AMPHIPOD *GAMMARUS LAWRENCIANUS*

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### ABSTRACT

A trade-off is found between growth and the length of time male amphipods (*Gammarus lawrencianus*) spend in amplexus. Males spending the majority of time in amplexus showed 45% less growth than unamplexed males. The inability of males to use their gnathopods to feed while in amplexus appears to cause this reduced growth. Growth rates of females appear unaffected by amplexus.

Since male size is correlated with male reproductive success in *G. lawrencianus*, a 45% decrease in size increment at the next molt would represent a similar loss in the incremental male reproductive success. Male mating decisions are therefore based not only on immediate past male investment in amplexus, male size, and population characteristics, but also on the trade-off between present reproduction and future size.

### INTRODUCTION

Reproduction in the marine amphipod *Gammarus lawrencianus* (Bousfield) follows a period of amplexus in which the male and female remain attached together. This precopulatory attachment is a form of "mate guarding," and is usually treated as an investment in time by the male (Parker, 1974).

Guarding of females has been examined in several species. Manning (1975) and Ridley and Thompson (1979) have investigated precopulatory guarding in isopods, Parker (1978) in the dung fly, Hartnoll and Smith (1978, 1980), Birkhead and Clarkson (1980), Wildish (1982), and Hunte *et al.* (in press) have all studied amplexus in amphipods, and Davies and Halliday (1977, 1979) in toads. In these cases, guarding of a female will be advantageous when the expected rate of gain in reproductive success due to amplexus is potentially greater than the sum of (1) the loss due to withdrawal for further searching (Parker, 1974, 1978; Hunte *et al.*, in press), (2) the increased risk of predation due to being a larger more visible target (Strong, 1973; VanDolah, 1978; Ridley and Thompson, 1979; Wildish, 1982), and (3) the physiological expense of amplexing owing to increased energy expenditure (Manning, 1975; Calow, 1979) or to a post-copulatory refractory period (Hunte *et al.*, in press).

Amphipod amplexus occurs when a sexually mature male comes into contact with a female and attempts to take hold. If successful, the male holds her close to his ventral surface by inserting his gnathopods between the segments along her anterior dorsal surface, then turning her around and carrying her longitudinally beneath him.

*G. lawrencianus* is a macrophageous feeder, feeding on coarse solid food which is grasped and manipulated by the gnathopods which are also used to hold the female during amplexus. Females appear to be able to exercise some choice of males

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during the early stages of amplexus, in that females large relative to the male can escape, providing a possible means of sexual selection for larger males. Doyle and Hunte (1981b), and Doyle and Myers (1982) have shown that female fecundity varies directly with size in *G. lawrencianus*.

This study had two aims: (1) to test for an effect of amplexus on the rate of food intake by both sexes, and (2) if a difference in feeding rate exists, to determine how much a reduction in growth may result from that difference. Since female fecundity is correlated with female size and hence with male size, a decrease in male growth rate represents a loss of future male reproductive success. Such a physiological cost to reproduction would cause a trade-off between present and future reproductive success which must be added to the time-budget considerations of Hunte *et al.* (in press).

## MATERIALS AND METHODS

### *Free and amplexed feeding rates*

Amphipods in all experiments were randomly collected from a laboratory-reared population (Doyle and Hunte, 1981a, b). Individual and amplexed amphipods were isolated without food in 25.0 ml petri dishes filled with sea water at 22°C, and having a fecal pellet trap composed of .75 mm plastic screening. After a 24 hour starvation period, the sea water was replaced and a weighed dry sample (2.000–3.500 mg) of 1200 dpm/mg <sup>14</sup>C-labeled cellulose suspended in coagulated egg white was added. The remaining food and fecal pellets were collected and the sea water replaced after 24 hours. A second 24-hour starvation period followed feeding.

Live amphipods were weighed on an electrobalance after blotting with absorbent paper. Each animal was then dissected and the gut with caecae, the body without head, tail, or gut, and the fecal pellets were placed in separate scintillation vials and dissolved in NCS Tissue Solubilizer.

Twenty-seven individual and 33 amplexed males as well as 27 individual and 29 amplexed females were so tested. Animals discarded because they molted, separated, or died are not included in the results. Ten individual males, 10 females, and 11 amplex pairs served as controls, fed with non-radioactive food.

### *Growth rates of free and amplexed males*

Two treatments were prepared, the first composed of "free" male amphipods and the second of male and female amphipods in a one-to-two ratio. The sex ratio in treatment two caused the males to remain in amplexus over much of the experimental period.

In each of 4 free male replicates, 21 males between 25.0 and 35.0 mg were collected, and their live weights determined. Five amplexed male replicates were prepared consisting of 7 males in the same weight range as above plus 14 females (smaller than the males).

Live weights of all males were determined on days 0, 9, 29, and 43 of the experiment. The experiment ended on the 44th day due to mortalities.

### *Growth rate of males without gnathopods*

Gnathopods were cut distal to the basis. Five replicates of this treatment and five uncut controls were prepared. Each of the control replicates contained 16 males between 10.0 and 20.0 mg. Two treatment replicates contained 17 males and the

others 16. All treatment replicates contained five females as well, which if found in amplexus indicated males with regenerated gnathopods. Checked daily, amplexed males had their gnathopods recut. Live weights of all male amphipods were determined every 9 days for 27 days. Examined under a microscope after weighing, gnathopods were recut if necessary.

## RESULTS

### *Free and amplexed feeding rates*

The results of the consumption of both free and amplexed female amphipods is given in Figure 1. The (Gut + Body) dpm data when linearly regressed against female weight shows a low, positive correlation in both cases. The equation describing the free female feeding rates has a slope  $U_f = 7.37$  (S.D. = 2.42,  $R^2 = .27$ ) while that of amplexed females is  $U_a = 7.6$  (S.D. = 3.05,  $R^2 = .19$ ). Although statistically significant, the  $R^2$  is low indicating only slight size dependency of feeding within the range of sizes studied. The low slopes and broadly overlapping size ranges of the two groups make adjustment for weight as a covariate unnecessary, and so a Kruskal-Wallis test (Sokal and Rohlf, 1981a) was used to test for a difference in (Gut + Body) dpm between amplexed and free females. There is no evidence to suggest that the activity measured in the two groups differed ( $\chi^2(1) = .620$ ,  $P > .05$ ). Female feeding rate appears to be independent of amplexus status and nearly independent of wet weight in this experiment.

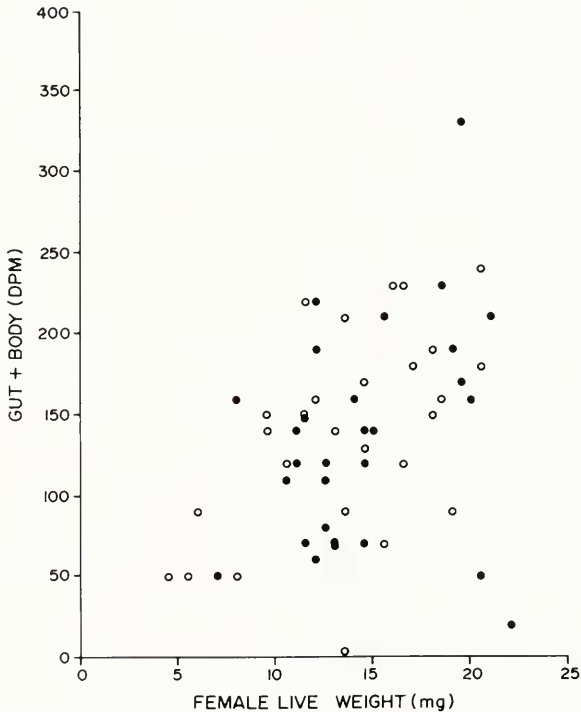


FIGURE 1. Food consumption over 24 h by free (open circles) and amplexed (closed circles) female amphipods.

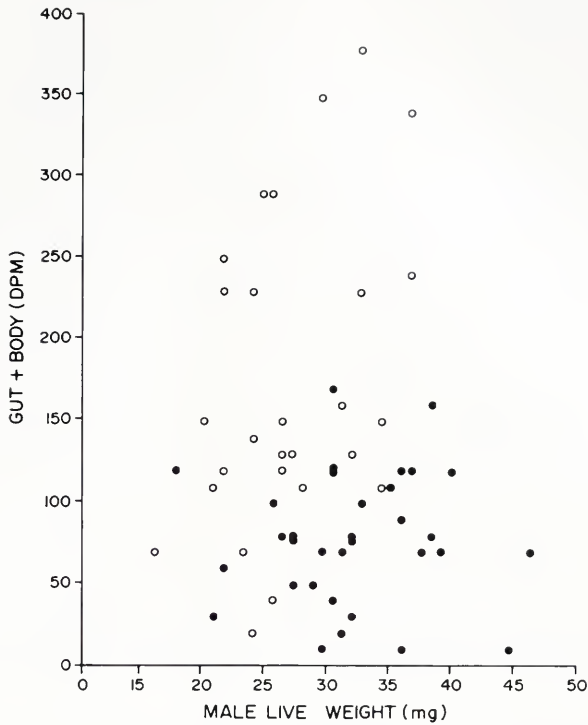


FIGURE 2. Food consumption over 24 h by free (open circles) and amplexed (closed circles) male amphipods.

Free and amplexed male feeding rates are shown in Figure 2. The slope of the linear equation of (Gut + Body) dpm regressed against male weight is  $U_f = 6.84$  (S.D. = 3.29,  $R^2 = .14$ ) and  $U_a = .0795$  (S.D. = 1.19,  $R^2 = 0$ ) for free and amplexed males respectively. Thus free male amphipod feeding rates are not significantly size-dependent. No correlation was shown between the calculated residuals of amplexed male consumption and either the female weight or the ratio of male to female weight, indicating that the feeding rate of amplexed males is independent of the size of the female carried. A Kruskal-Wallis analysis of this data indicates that male guarding of a female reduced male feeding rate ( $\chi^2(1) = 22.5$ ,  $P < .005$ ) by 53%.

#### *Growth rates of free and amplexed males*

The divergence of the mean weights of the two treatments is shown in Figure 3. A two-way analysis of variance (factors; amplexed state by replicate and period, Sokal and Rohlf, 1981b) of the increment of weight increase over the first 9 day period, second 20 day period, and final 14 day period is given in Table I.

Amplexed males in this experiment grew at a rate 45% less than that of free males. All factors, male state, period of growth, and the interaction between the two are significant, although the last less so than the first two.

#### *Growth rate of males without gnathopods*

The change in mean weight of these two treatments over 27 days is shown in Figure 4. The results of a two-way ANOVA (with three 9-day periods) are given in

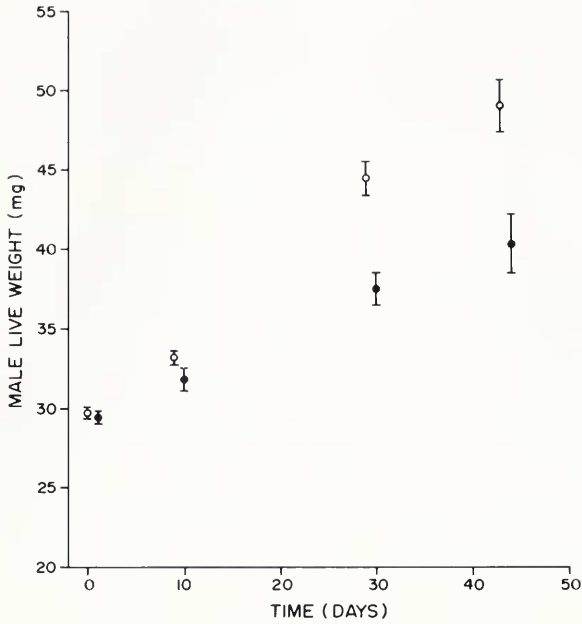


FIGURE 3. Growth of free (open circles) and amplexed (closed circles) male amphipods over 43 days.

Table II. They indicate, with a high degree of significance, that males with gnathopods grew 44% faster than those who had had them removed.

#### DISCUSSION

Mate guarding is advantageous to a male when the cost of amplexus is less than the return in reproductive success to that male (Parker, 1974). The results (Fig. 3) indicate that a major physiological cost incurred by amplexing males is reduced growth. The close correspondence between the growth lost in amplexus and the decrease following gnathopod removal indicates that amplexus in *G. lawrenciamus* has a cost not so much in energy expended to carry a female, but in reduced food consumption by the male.

TABLE I

ANOVA table of growth of free and amplexed males over three periods

Source of variation	df	ss	F <sub>s</sub>
Subgroups	5	232.9	12.7**
A (Time period)	2	145.6	19.9**
B (Amplexus status)	1	59.1	16.1**
A × B (Interaction)	2	28.2	3.84*
Within subgroup error	18	66.0	
Total	23	298.8	

\* 0.01 < P < 0.05.

\*\* P < 0.001.

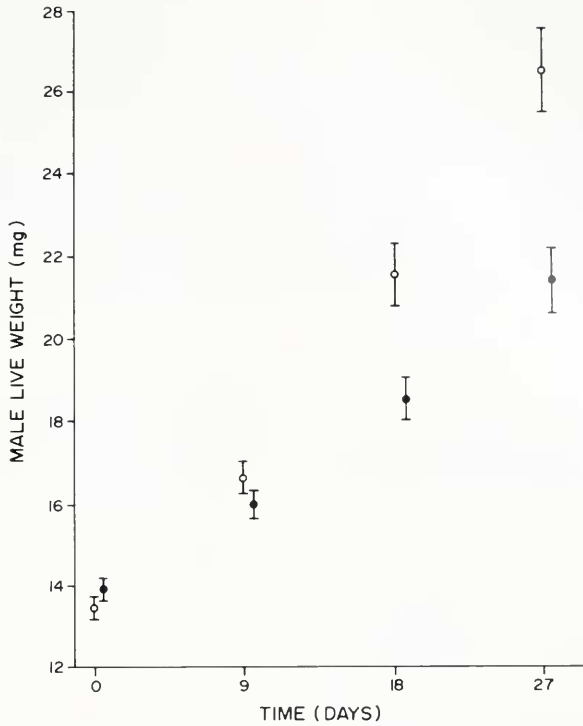


FIGURE 4. Growth of male amphipods with (open circles) and without (closed circles) gnathopods over 27 days.

Size-assortive mating is caused by (1) larger female amphipods selecting for larger mates by escaping smaller males more often (Ridley and Thompson, 1979), and (2) larger males preferentially mating with larger females (Manning, 1975; Birkhead and Clarkson, 1980; Hunte *et al.*, in press). Since larger females are more fecund (Doyle and Hunte, 1981b; Doyle and Myers, 1982), larger male amphipods on average will produce more offspring than smaller males in any one successful mating.

TABLE II

*ANOVA table of growth of males with and without gnathopods over three 9-day periods*

Source of variation	df	ss	F <sub>s</sub>
Subgroups	5	38.6	5.52*
A (Time period)	2	6.07	2.17
B (Gnathopod status)	1	31.1	22.2**
A × B (Interaction)	2	1.44	0.514
Within subgroup error	24	33.6	
Total	29	72.2	

\*  $0.005 < P < 0.001$ .

\*\*  $P > 0.001$ .

The optimal duration of amplexus depends on population characteristics such as mortality rate, sex ratios, and male and female size distribution (Hunte *et al.*, in press). Since the relations between male and female size and female fecundity are reasonably linear, a 45% decrease in size increment at the next molt would represent a similar loss in the incremental male reproductive success (measured as the number of eggs fertilized).

In their examination of *G. lawrencianus*, Hunte *et al.* (in press) determined that immediate past male investment in amplexus may influence mating decisions through change in physiological state (*e.g.*, a post-amplexus refractory period). We now observe that the situation is complicated by yet another factor, a trade-off between present reproduction and future size, as modulated by feeding activity during amplexus.

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